NEOTROPICAL BIOLOGY AND CONSERVATION

Neotropical Biology and Conservation
17(1): 87–102 (2022)
doi: 10.3897/neotropical.17.e79247

RESEARCH ARTICLE

The importance of pollination and dispersal syndromes for the conservation of Cerrado Rupestre fragments on ironstone outcrops immersed in an agricultural landscape

Cássio Cardoso Pereira[1], Daniel Meira Arruda[2], Fernanda de Fátima Santos Soares[3], Rúbia Santos Fonseca[4]

1 *Universidade Federal de Minas Gerais, Departamento de Génetica, Ecologia e Evolução, Programa de Pós Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Belo Horizonte, MG, Brazil*
2 *Universidade Federal de Minas Gerais, Instituto de Geociências, Belo Horizonte, MG, Brazil*
3 *Southwest Baptist University, Department of Healthy Sciences, Springfield, MO, USA*
4 *Universidade Federal de Minas Gerais, Instituto de Ciências Agrárias, Montes Claros, MG, Brazil*

Corresponding author: Cássio Cardoso Pereira (cassiocardosopereira@gmail.com)

Academic editor: Patricia Nunes-Silva | Received 18 December 2021 | Accepted 9 March 2022 | Published 22 March 2022

Citation: Pereira CC, Arruda DM, Santos Soares FF, Fonseca RS (2022) The importance of pollination and dispersal syndromes for the conservation of Cerrado Rupestre fragments on ironstone outcrops immersed in an agricultural landscape. Neotropical Biology and Conservation 17(1): 87–102. https://doi.org/10.3897/neotropical.17.e79247

Abstract

Studies on pollination and seed dispersal are essential for the conservation of plant diversity. In this study, we aimed to evaluate the pollination and dispersal syndromes of five fragments of the Cerrado Rupestre immersed in an agricultural landscape to answer the following questions: (i) What is the frequency of pollination and dispersal syndromes among species and individuals?; (ii) Which are the predominant pollination and seed dispersal syndromes in this environment?. A total of 66 species, belonging to 44 genera and 29 botanical families, were evaluated. Melittophily was the most common type of pollination syndrome, observed in 54.55% of the species, followed by phalenophily (9.09%), cantharophily, ornithophily, quiropterophilly and sphingophily (all 3.03%), and psychophilly (1.51%). Generalist pollination represented 22.73% of the records. Of the 1246 individuals identified, 59.23% were melitophilous, 25.20% generalists, 5.86% phalenophilous, 3.37% quiropterophilous, 2.49% cantharophilous, 2.25% ornithophilous, 1.44% sphingophilous and 0.16% psychophilous. Regarding dispersion syndromes, zoochory was the most common type of dispersion, observed in 68.18% of the species, followed by anemochory (28.79%) and autochory (3.03%). On the other hand, the frequency among individuals differed from the values found for frequency among species. Of the 1246 individuals identified,

55.38% were anemochoric, 43.10% zoochoric, and 1.52% autochoric. Our results demonstrate the predominance of biotic syndromes in the community, especially melittophily and zoochory, contributing to a better understanding of the functionality and availability of resources in the community, as well as indispensable information for the conservation, management, and restoration of natural environments.

Keywords
anemochory, bees, canga, fruits, melittophily, neotropical savanna, zoochory

Introduction

The reproduction in plant species involves many steps, and genetic diversity is influenced by pollinators and dispersers that promote gene flow (Nason et al. 1998). Pollination is a fundamental process in communities, being an essential prerequisite for the reproduction of angiosperms and for the development of fruits and seeds that will be dispersed (Ollerton 2021). It is a mutualistic process of interaction between plants and pollinators, where the partners of this interaction maximize their survival and reproductive success (Ollerton 2021).

Many floral characteristics may reflect adaptive responses to selection by pollinators, that is, some plant species may have characteristic floral phenotypes that are more adapted to more effective or frequent pollinators (Danieli-Silva et al. 2012; Rosas-Guerrero et al. 2014), present more generalized characteristics, influenced by mixtures of pollinators of different functional types, or even present characteristics (i.e. influenced by mixtures of pollinators of different functional types) or floral phenotypes in response to antagonistic insects (Ollerton et al. 2009). Thus, patterns of these plant-pollinator interactions can be characterized as pollination syndromes (Faegri and van der Pijl 1979), which are characterized according to the floral morphology and floral features that attract potential pollinators and the co-evolutionary and interdependent relationship between them (Rosas-Guerrero et al. 2014). Among the main pollination syndromes, we highlight the pollination by wind (anemophily), by birds (ornithophily), by bats (quiropterophilly), by bees (melittophily), beetles (cantharophily), flies (myophily), butterflies (psychophily), sphingids (sphingophily) and moths (phalenophily) (Faegri and van der Pijl 1979).

The frequency of pollination syndromes can vary according to several factors such as vegetation types and their plant strata (e.g., Quirino and Machado 2014; Diogo et al. 2016). Insects, especially bees, are agents present in all plant strata, constituting important pollination resources throughout the entire vertical space occupied by the shrub and arboreal components of forests and savannas (Silva et al. 2012). On the other hand, syndromes such as ornithophily and quiropterophilly, generally occur more frequently on more open edges and formations, perhaps because bats and birds need open spaces to fly (Yamamoto et al. 2007).

After pollination and successful reproduction, plants also adopt different strategies to disperse their fruits and seeds and guarantee seedling survival (Schupp and Fuentes 1995; Wunderlee 1997; Galetti et al. 2013). Plant species have developed several adaptive strategies related to increased dispersal of propagules in response

to associated selective pressure and the highest mortality rate that occurs close to the mother plant. In this way, they can develop mechanisms that allow diaspores to escape conditions that can lead to mortality near the mother plant, where predation, pathogen abundance, and competition are highest (Janzen 1971). However, a more intense seed rain near the mother plant could offset the mortality factors density-dependent, promoting higher recruitment of individuals (Hubbell 1980). Thus, successful dispersal determines the species composition and abundance of a community (Schupp and Fuentes 1995). According to van der Pijl (1982), plants disperse their fruits in three main ways: anemochory, when the diaspore is endowed with structures that provide transport by the wind; autochory, when the plant has its mechanisms for the release of fruits or seeds; and zoochory, whose diaspores have a set of characters that favor dispersion by animals. The latter is characterized by being a more complex syndrome, which, depending on the fauna, is associated with more stable/conserved communities or ones more sensitive to disturbances (Galetti et al. 2013).

The frequency of dispersion syndromes can also vary between different environments (Carvalho 2010; Diogo et al. 2016). In the Neotropics, the proportion of zoochoric species decreases from wet areas to dry areas, where abiotic vectors become more important (Gentry 1982). According to Howe and Smallwood (1982), anemochory predominates in seasonal open canopy environments, such as in the cerrado *sensu stricto*. In this context, it is expected that savanna environments present lower frequencies of zoochoric species than areas of humid forests, where zoochory predominates (Munhoz and Felfili 2005).

Studies on pollination and seed dispersal are essential for the conservation of plant diversity in the tropics and to supply the consumption demands of populations (Resende et al. 2019). Currently, the Cerrado domain comprises the region with the largest agricultural production in Brazil (Lambers et al. 2020). Anthropogenic pressure on this vegetation intensified in the 1970s, contributing to the intense fragmentation of this environment (Morandi et al. 2020). As a result, the remnants of vegetation are restricted to non-farmable areas, such as hilltops, mountain slopes, and some riparian forests (Silveira et al. 2016). Thus, describing the composition of plant species and reproductive biology becomes increasingly essential for the preservation of the remaining areas of the Cerrado and the maintenance of ecosystem services that are so essential for people's health and quality of life (Resende et al. 2019).

In this study, we aimed to evaluate the pollination and dispersal syndromes of five fragments of the Cerrado Rupestre immersed in an agricultural landscape to answer the following questions: (i) What is the frequency of pollination and dispersal syndromes among species and individuals belonging to fragments?; (ii) Which are the predominant pollination and seed dispersal syndromes in this environment? These questions would bring evidence about the interactions between the vegetation community, flower visitors, and seed dispersers who could emphasize the need to preserve the fragmented vegetation. In this way, we approach the patterns of species and individuals of several botanical families through a floristic survey, determining the frequency of pollination and dispersal syndromes among plant species and also among the individuals present in these fragments.

Methods

Study site

The study was carried out in Rio Paranaíba, Minas Gerais, Brazil (19°11'38"S, 46°14'49"W, Fig. 1A), a municipality inserted in the Cerrado Domain, which presents a highly technified agricultural production. The average altitude of the municipality is 1200 m, and the region's climate is classified as Tropical Altitude (Cwa), with two well-defined seasons: the rainy season from October to April, and the dry season from May to September (Alvares et al. 2013).

Five fragments of Cerrado Rupestre were studied, predominantly composed of a continuous crust of canga, also known as "canga couraçada" (Jacobi and Carmo 2008). The types of canga observed in these areas form a rigid layer on the ground, with the roots accessing the soil through cracks or settling in rock crevices (Pereira et al. 2019). All fragments have between 10 and 15 ha, are at an altitude between 1150 and 1250 meters, and are close to the urban area. In addition, as they are located on slopes and hilltops, they are characterized as "Permanent Preservation Areas" (PPAs), representing important remnants of the municipality that persist in agricultural landscapes. The coordinates of the five studied fragments are: fragment 1 = 19°20'55"S, 46°25'81"W; fragment 2 = 19°18'63"S, 46°27'30"W; fragment 3 = 19°18'37"S, 46°25'36"W; fragment 4 = 19°18'65"S, 46°23'62"W; and fragment 5 = 19°16'69"S, 46°22'93"W (For more details on these fragments, see Fig. 1B and Pereira et al. 2019).

Data sampling

In December 2013, 10 random plots of 0.01 ha (10 × 10 m) were allocated, totaling 0.5 ha in each sampled fragment. (Eisenlohr et al. 2015). All individuals with

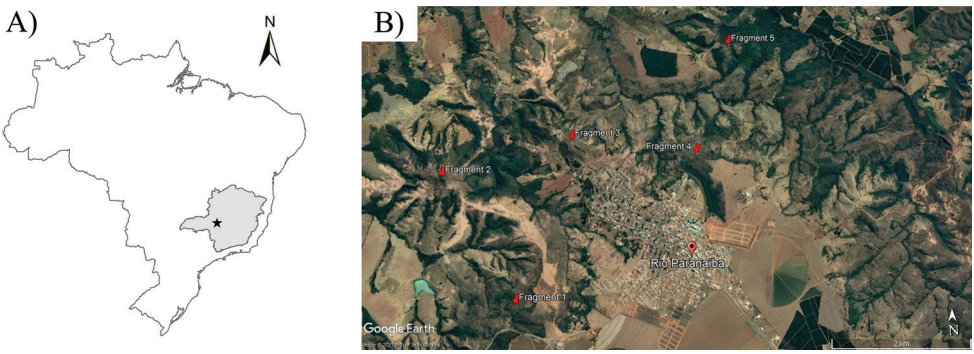

Figure 1. Geographic location (**A**) and an aerial image of the municipality of the Rio Paranaíba (**B**), Minas Gerais, south-eastern Brazil, showing the five fragments of Cerrado Rupestre studied (image: Google Earth 2021). The fragments evaluated are found on slopes and hilltops, being "Permanent Preservation Areas" (PPAs), and are composed of ferruginous soil that forms a continuous crust known as "canga couraçada".

basal stem diameters (BSD) ≥ 3 cm were sampled to obtain species abundance and richness. Dead individuals were not included in our sample. The period of the year (rainy period) did not interfere with the species identification. We identified the species in the field and also had the help of specialists. The nomenclature of the species was according to the species list of the Flora do Brasil (2020).

The life forms of the plant species were classified according to Mendonça et al. (2008). As for pollination syndromes, plant species were classified according to Faegri and van der Pijl (1979): cantharophily, melittophily, ornithophily, phalenophily, psychophilly, quiropterophilly, sphingophily.

Because many species of pollinators can visit the same plant, especially in the absence of resources, the use of pollination syndromes has been the subject of much discussion in the literature, and their use requires caution (Ollerton et al. 2009). However, studies reporting floral syndromes are valid because they indicate that floral evolution is convergent and driven by adaptation to the most effective pollinator group (Danieli-Silva et al. 2012; Rosas-Guerrero et al. 2014). In this way, we classified plant species within specific floral syndromes when the pollinating agents did not vary between the literature consulted or were the most frequent in the pollination of species (thus considered being the main pollinators, see Rosas-Guerrero et al. 2014). However, plant species with floral characteristics that do not fit these classifications and that do not have a main pollinator reported in the literature, being pollinated by several taxons, were classified as generalists.

The types of fruits were classified according to Barroso et al. (1999) and the classification of diaspore dispersion syndromes according to fruit morphology followed the categories proposed by van der Pijl (1982): anemochoric, zoochoric, and autochoric species.

Information about pollination and dispersal syndromes was obtained from the literature (Barroso et al. 1999; Pinheiro and Ribeiro 2001; Gottsberger and Silberbauer-Gottsberger 2006; Kinoshita et al. 2006; Yamamoto et al. 2007; Barbosa and Sazima 2008; Ishara et al. 2008; Kuhlmann and Fagg 2012; Rosas-Guerrero et al. 2014; Kuhlmann and Ribeiro 2016) and in field samples.

Data exploration

We extract frequency data regarding life form, fruit type, pollination and dispersal syndromes, and we build pie charts on these syndromes to explore our data. All analyses were conducted using R base package on R software (R Core Team 2021).

Results

A total of 66 species, belonging to 44 genera and 29 botanical families, were evaluated. Regarding life forms, most species studied were trees (57.58%), followed by small trees (25.76%), shrubs (15.15%), and sub-shrubs (1.51%) (Table 1).

Table 1. Plant species abundances, life form, fruit type, and pollination and dispersion syndromes at the five fragments of Cerrado Rupestre immersed in an agricultural landscape in Rio Paranaíba, Minas Gerais. N° ind.: number of individuals; cantharophily: beetle pollination; generalist: pollination by many groups of pollinators; melittophily: bee pollination; ornithophily: bird pollination; phalenophily: moth pollination; psychophilly: butterfly pollination; quiropterophilly: bat pollination; sphingophily: hawk moth pollination; anemochory: wind dispersal; autochory: dispersion carried out by the plant itself; zoochory: animal dispersal.

Family/Species	Fragments (n° ind.)						Life form	Fruit	Pollination	Dispersion
	1	2	3	4	5	Total				
Annonaceae										
Annona coriacea Mart.	2	0	1	6	1	10	tree	fleshy	cantharophily	zoochory
Xylopia sericea A.St.-Hil	0	0	21	0	0	21	tree	fleshy	cantharophily	zoochory
Apocynaceae										
Hancornia speciosa Gomes	1	11	1	1	0	14	tree	fleshy	sphingophily	zoochory
Aspidosperma tomentosum Mart.	1	12	13	17	22	65	tree	dry	phalenophily	anemochory
Asteraceae										
Piptocarpha rotundifolia (Less.) Baker	0	0	0	2	0	2	subtree	dry	psychophily	anemochory
Bignoniaceae										
Handroanthus ochraceus (Cham.) Mattos	0	0	0	1	0	1	tree	dry	melittophily	anemochory
Calophyllaceae										
Kielmeyera petiolaris Mart.	14	0	0	0	14	28	tree	dry	melittophily	anemochory
Caryocaraceae										
Caryocar brasiliense Cambess.	1	4	0	0	1	6	tree	fleshy	quiropterophilly	zoochory
Celastraceae										
Plenckia populnea Reissek	18	3	4	0	18	43	tree	fleshy	melittophily	zoochory
Chrysobalanaceae										
Couepia grandiflora (Mart. & Zucc.) Benth.	1	0	0	0	1	2	tree	fleshy	phalenophily	zoochory
Combretaceae										
Terminalia argentea Mart.	0	0	1	0	0	1	tree	dry	generalist	anemochory
Connaraceae										
Connarus suberosus Planch.	1	3	0	2	1	7	tree	fleshy	generalist	zoochory
Erythroxylaceae										
Erythroxylum campestre A.St.-Hil.	3	0	0	0	0	3	subshrub	fleshy	generalist	zoochory
Erythroxylum daphnites Mart.	78	35	30	38	10	191	subtree	fleshy	generalist	zoochory
Erythroxylum tortuosum Mart.	13	5	6	10	0	34	subtree	fleshy	generalist	zoochory
Erythroxylum sp.	0	1	0	0	0	1	subtree	fleshy	generalist	zoochory
Euphorbiaceae										
Pera glabrata (Schott) Poepp. ex Baill.	1	0	0	0	0	1	tree	fleshy	generalist	zoochory
Fabaceae										
Dalbergia miscolobium Benth.	41	106	92	35	89	363	tree	dry	melittophily	anemochory
Enterolobium gummiferum (Mart.) J.F.Macbr.	2	0	0	0	0	2	tree	dry	melittophily	zoochory
Fabaceae sp.	3	0	0	0	0	3	tree	dry	melittophily	anemochory
Machaerium villosum Vogel	8	0	0	1	0	9	tree	dry	melittophily	anemochory
Machaerium opacum	0	2	0	0	0	2	tree	dry	melittophily	anemochory
Machaerium sp.	0	0	0	1	1	2	tree	dry	melittophily	anemochory
Stryphnodendron adstringens (Mart.) Coville	8	2	5	3	0	18	tree	dry	generalist	zoochory
Lamiaceae										
Aegiphila lhotzkiana Cham.	0	0	1	0	1	2	tree	fleshy	melittophily	zoochory
Lythraceae										
Lafoensia pacari A.St.-Hil.	22	1	4	8	1	36	tree	dry	quiropterophilly	anemochory
Malpighiaceae										
Banisteriopsis sp.	3	0	0	0	0	3	shrub	dry	melittophily	anemochory
Banisteriopsis malifolia (Nees & Mart.) B.Gates	0	0	4	2	8	14	shrub	dry	melittophily	anemochory
Byrsonima coccolobifolia Kunth	1	1	0	0	0	2	tree	fleshy	melittophily	zoochory
Byrsonima crassifolia (L.) Kunth	4	0	0	0	0	4	tree	fleshy	melittophily	zoochory
Byrsonima verbascifolia (L.) DC.	7	0	0	2	0	9	tree	fleshy	melittophily	zoochory
Heteropterys byrsonimifolia A.Juss.	0	9	11	0	0	20	shrub	dry	melittophily	anemochory

Family/Species	Fragments (n° ind.)						Life form	Fruit	Pollination	Dispersion
	1	2	3	4	5	Total				
Byrsonima sp.	1	0	0	0	0	1	shrub	fleshy	melittophily	zoochory
Melastomataceae										
Miconia albicans (Sw.) Triana	3	4	2	6	0	15	shrub	fleshy	melittophily	zoochory
Miconia sp. 1	6	0	0	0	0	6	shrub	fleshy	melittophily	zoochory
Miconia sp. 2	1	0	0	0	0	1	shrub	fleshy	melittophily	zoochory
Meliaceae										
Cabralea canjerana (Vell.) Mart.	0	1	0	0	0	1	tree	fleshy	phalenophily	zoochory
Myristicaceae										
Virola sebifera Aubl.	0	2	14	0	12	28	tree	fleshy	generalist	zoochory
Myrtaceae										
Blepharocalyx salicifolius(Kunth) O.Berg	0	0	1	0	0	1	subtree	fleshy	melittophily	zoochory
Eugenia sp. 1	0	0	5	0	0	5	subtree	fleshy	melittophily	zoochory
Eugenia sp. 2	0	1	11	3	4	19	subtree	fleshy	melittophily	zoochory
Myrcia lingua (O.Berg) Mattos	1	0	0	0	0	1	subtree	fleshy	melittophily	zoochory
Myrcia splendens (Sw.) DC.	4	0	14	0	0	18	subtree	fleshy	melittophily	zoochory
Myrcia variabilis DC.	3	0	0	0	0	3	subtree	fleshy	melittophily	zoochory
Myrcia sp.	0	0	0	0	1	1	subtree	fleshy	melittophily	zoochory
Myrtaceae sp. 1	0	0	0	1	0	1	subtree	fleshy	melittophily	zoochory
Myrtaceae sp. 2	5	3	0	0	0	8	subtree	fleshy	melittophily	zoochory
Myrtaceae sp. 3	1	0	0	0	0	1	subtree	fleshy	melittophily	zoochory
Psidium pohlianum O. Berg	0	0	1	0	0	1	subtree	fleshy	melittophily	zoochory
Nyctaginaceae										
Guapira noxia (Netto) Lundell	6	5	0	1	0	12	tree	fleshy	generalist	zoochory
Neea theifera Oerst.	1	0	0	0	0	1	subtree	fleshy	generalist	zoochory
Ochnaceae										
Ouratea castaneifolia (DC.) Engl.	0	0	0	1	0	1	subtree	fleshy	melittophily	zoochory
Proteaceae										
Roupala montana Aubl.	1	0	1	0	0	2	tree	dry	phalenophily	anemochory
Rubiaceae										
Palicourea rigida Kunth	14	3	0	3	1	21	shrub	fleshy	ornithophily	zoochory
Rudgea viburnoides (Cham.) Benth.	2	0	0	0	0	2	tree	fleshy	generalist	zoochory
Tocoyena formosa (Cham. & Schltdl.) Schum.	4	0	0	0	0	4	shrub	fleshy	sphingophily	zoochory
Rutaceae										
Spiranthera odoratissima A.St.-Hil.	1	0	0	0	0	1	tree	dry	phalenophily	autochory
Zanthoxylum riedelianum	0	0	0	1	0	1	tree	fleshy	generalist	zoochory
Sapotaceae										
Pouteria ramiflora (Mart.) Radlk.	0	0	2	0	0	2	tree	fleshy	generalist	zoochory
Pouteria torta (Mart.) Radlk.	0	0	0	5	7	12	tree	fleshy	generalist	zoochory
Solanaceae										
Solanum lycocarpum A.St.-Hil.	0	0	0	0	3	3	shrub	fleshy	melittophily	zoochory
Styracaceae										
Styrax ferrugineus Nees & Mart.	3	0	0	12	0	15	tree	fleshy	melittophily	zoochory
Vochysiaceae										
Qualea grandiflora Mart.	1	0	0	0	1	2	tree	dry	phalenophily	anemochory
Qualea multiflora Mart.	39	17	46	10	15	127	tree	dry	melittophily	anemochory
Qualea parviflora Mart.	3	0	0	0	0	3	tree	dry	melittophily	anemochory
Vochysia thyrsoidea Pohl	7	0	0	0	0	7	tree	dry	ornithophily	anemochory

Pollination

In all life forms, melittophily was the predominant mode of pollination, occurring in 42.11% of trees, 80.00% of shrubs, and 70.59% of small trees. The only sub-shrubs species was melitophilous (Table 1).

Melittophily was the most common type of pollination syndrome, observed in 54.55% of the species, followed by phalenophily (9.09%), cantharophily, ornithophily, quiropterophilly and sphingophily (all 3.03%), and psychophilly (1.51%). Generalist pollination represented 22.73% of the records (Fig. 2A). Bee pollination also predominated among families, being present in 12 families (41.28%) and being exclusive in ten of them (34.48%). Among the families sampled in this study, Rubiaceae and Vochysiaceae presented the highest diversity of syndromes (Table 1).

The frequency of pollination syndromes among individuals differed from the values found for frequency among species. Of the 1246 individuals identified, 59.23% were melitophilous, 25.20% generalists, 5.86% phalenophilous, 3.37% quiropterophilous, 2.49% cantharophilous, 2.25% ornithophilous, 1.44% sphingophilous and 0.16% psychophilous (Fig. 2C). Melittophily was the dominant syndrome among most individuals, predominating in all fragments (Table 1).

Seed dispersal

In all life forms, zoochory was the predominant dispersal syndrome, occurring in 55.26% of trees, 70.00% of shrubs, and 94.12% of small trees. The only subshrub species was zoochoric. Among the 66 species sampled in the Cerrado Rupestre, 44 species (66.67%) had fleshy fruits, all zoochorous, and 22 species (33.33%) had dry fruits. Species with dry fruits are predominantly anemochoric or autochoric, except for *Enterolobium gummiferum* (Fabales, Fabaceae), which is zoochoric (Table 1).

Zoochory was the most common type of dispersion, observed in 68.18% of the species, followed by anemochory (28.79%) and autochory (3.03%) (Fig. 2B). Furthermore, this dispersion syndrome predominated in all fragments and species of most other families, except for Asteraceae, Bignoniaceae, Calophyllaceae, Combretaceae, Lythraceae, Proteaceae, and Vochysiaceae, composed exclusively of anemochoric species. Among the families sampled in this study, Fabaceae showed the highest diversity of syndromes, with zoochoric, anemochoric, and autochoric species. The Fabaceae and Rutaceae families were the only ones that presented autochoric species (Table 1).

The frequency of dispersion syndromes among individuals differed from the values found for frequency among species. Of the 1246 individuals identified, 55.38% were anemochoric, 43.10% zoochoric and 1.52% autochoric (Fig. 2D). Differences in the frequency of zoochory were observed between individuals in the fragments: this syndrome predominated in fragments 1 and 4, and anemochory in fragments 2, 3 and 5 (Table 1).

Dalbergia miscolobium, melitophilous and anemochoric, was the most abundant plant species with 363 individuals, followed by *Erythroxyllum daphnitis* (Malpighiales, Erythroxylaceae) (generalist and zoochoric pollination, n = 191) and *Qualea multiflora* (Myrtales, Vochysiaceae) (melitophilous and anemochoric, n = 127).

Regarding the five fragments, *Dalbergia miscolobium* (Fabales, Fabaceae) was the most abundant species in fragments 2, 3, and 5, while *E. daphnitis* was the most abundant in fragments 1 and 4, in addition to being the most frequent zoochoric species in the Cerrado Rupestre of Rio Paranaíba (Table 1).

Discussion

Our results demonstrate the predominance of biotic syndromes in the community, especially melittophily and zoochory, while most individuals, corresponding to species with high dominance, characterize the typical pattern of the predominance of anemochory in this vegetation.

Pollination systems encompassed several groups of animals, being represented by more frequent and less frequent syndromes in these environments. The Cerrado Rupestre studied has a higher frequency of species and individuals potentially pollinated by bees, highlighting the importance of this group of pollinators in the fruiting of most species studied. Bees pollinate about 70% of plants in the Cerrado (Rabeling et al. 2019) and are also the largest pollinators of crops, responsible for increasing the quality and quantity of vegetable seed production, pastures, grains, and fruits (Yamamoto et al. 2010; Patel et al. 2021). This expressiveness is justified by the fact that bees use all resources: pollen, nectar, oil, and resin (Rabeling et al. 2019). Thus, melittophily was the predominant syndrome in several plant families that offered resources such as pollen (for example, Fabaceae, Melastomataceae, and Myrtaceae) and oil (Malpiguiaceae) (Rosas-Guerrero et al. 2014).

The other entomophilic syndromes were less expressive, but many plant species presented a generalized pollination system since their flowers can be pollinated by different generalist pollinators. Even when they are not the main food sources for these insects, the resources offered by these plants can be vital for the persistence of populations of these pollinators in the absence of other sources (Waser et al. 1996; Rabeling et al. 2019). Furthermore, this strategy can compensate for the fruiting of several plants in a possible seasonal insect deficiency (Waser et al. 1996).

On plant communities in the Cerrado, ornithophily and quiropterophilly represent less than 5% of all angiosperm species (Rabeling et al. 2019). These syndromes are strongly related to specific taxa, especially bromeliads (Rocca and Sazima 2010) and cactuses (Cordero-Schmidt et al. 2021), respectively. In the present study, ornithophily was observed in plant species with red or yellow tubular diurnal flowers with large amounts of nectar, on *Palicourea rigida* (Gentianales, Rubiaceae) (see Fig. 3A) and *Vochysia thyrsoidea* (Myrtales, Vochysiaceae). On the other hand, quiropterophilly was associated with *Caryocar brasiliensis* (Malpighiales, Caryocaraceae) and *Lafoensia pacari* (Myrtales, Lythraceae), species with white and yellow flowers of nocturnal anthesis, with a strong odor (characteristic of fermentation).

Regarding the dispersion of diaspores, our results also suggest the importance of fauna for maintaining the diversity of this community, with a predominance of zoochoric species. The highest frequency of zoochoric species observed in the

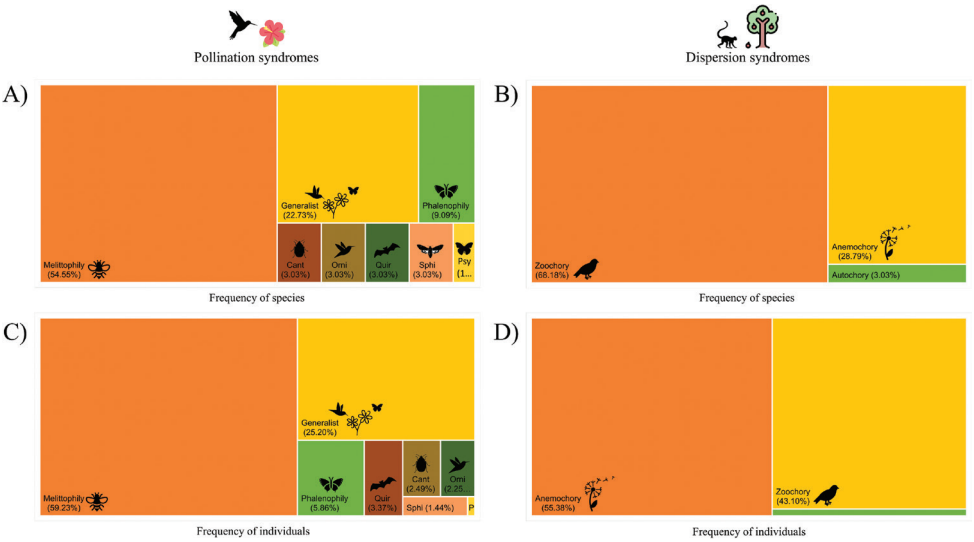

Figure 2. Frequency of pollination (**A**) and dispersal (**B**) syndromes between plant species and individuals (**C** and **D**, respectively) found in the five fragments of Cerrado Rupestre immersed in an agricultural landscape in Rio Paranaíba, Minas Gerais. **A:** Cant = Cantharophily, Orni = Ornithophily, Quir = Quiropterophilly, Sphy = Sphingophily, Psy = Psychophily (1.51%). **C:** P = Psychophily (0.16%). **D:** Green frame = Authocory (1.52%). Cantharophily: beetle pollination; generalist: pollination by many groups of pollinators; melittophily: bee pollination; ornithophily: bird pollination; phalenophily: moth pollination; psychophilly: butterfly pollination; quiropterophilly: bat pollination; sphingophily: hawk moth pollination; anemochory: wind dispersal; autochory: dispersion carried out by the plant itself; zoochory: animal dispersal.

present study (69.6%) was also found in studies carried out in savanna environments (Vieira et al. 2002; Martins et al. 2004; Toppa et al. 2004) and in forest environments (Yamamoto et al. 2007). These results demonstrate that when analyzing the frequency of syndromes among species, there may also be a predominance of zoochory in open environments such as those found in the Cerrado.

The predominance of zoochory may indicate the importance of fauna for plant species in this community. One of the hypotheses to explain the advantages of dispersal by animals is that of colonization and directed dispersal, that is, zoochory allows for the dispersal of larger seeds and, at the same time, it may be more effective than anemochory (Howe and Smallwood 1982; Vander Wall and Longland 2004). Animals commonly move between different habitats, being able to distribute larger amounts of seeds of different plant species. On the other hand, anemochoric and autochoric species depend on random events to disperse their seeds. This unpredictability can cause a smaller number of seeds to be distributed in habitats, or mean that distribution is less effective in distancing themselves from the mother plant (Schupp et al. 2010), despite the advantage of not depending on the availability of biotic agents for dispersion of its diaspores (Howe and Smallwood 1982).

Fleshy fruits, such as berries and drupes (e.g., *E. daphnitis*, second most abundant species in the study, N = 191), are often edible and therefore highly attractive, especially for birds (Fig. 3B), which favors the dispersion (Amico and Aizen 2005; Kuhlmann and Ribeiro 2016). However, dry fruits can also indicate zoochoric dispersion, when they have special mechanisms (Howe and Smallwood 1982; Kuhlmann and Ribeiro 2016), as is the case of the *E. gummiferum* fruit, which is dry and indehiscent, but has a spongy pulp with a strong odor, attracting mammals (Françoso et al. 2014). This wide morphological variation of fruits in the same syndrome reveals the variety of strategies that plants have to attract different dispersers, which, in turn, can benefit from the greater availability of food resources (Valenta and Nevo 2020).

On the other hand, when analyzing the frequency of syndromes among individuals, the predominance of anemochory in the Cerrado Rupestre fragments demonstrates the expected pattern for a seasonal and open environment (Howe and Smallwood 1982; Kuhlmann and Ribeiro 2016). This result shows that abundance is the best indicator of the real availability of resources, such as zoochorous fruits for fauna. This analysis, however, is not commonly done and we suggest with this study that the abundance of species in communities should receive more attention to better understand the distribution of these syndromes in these environments.

The variety of flowers and the availability of fruits in the Cerrado Rupestre, mainly zoochorous, indicate the need for preservation and studies on the degree of dependence of these plants on these animals. Thus, an important next step to be taken is to know the identity of these pollinators and dispersers to understand the role of animal species in the structure of these plant communities (Rabeling et al. 2019; Dellinger 2020; Borchardt et al. 2021). Plant-animal interactions are at the origin and maintenance of diversity and affect the functioning of ecosystems (Fuster and Traveset 2020). Furthermore, the pollination deficit can impact agriculture (Bauer and Wing 2010) and the dynamics of natural systems with variable importance ac-

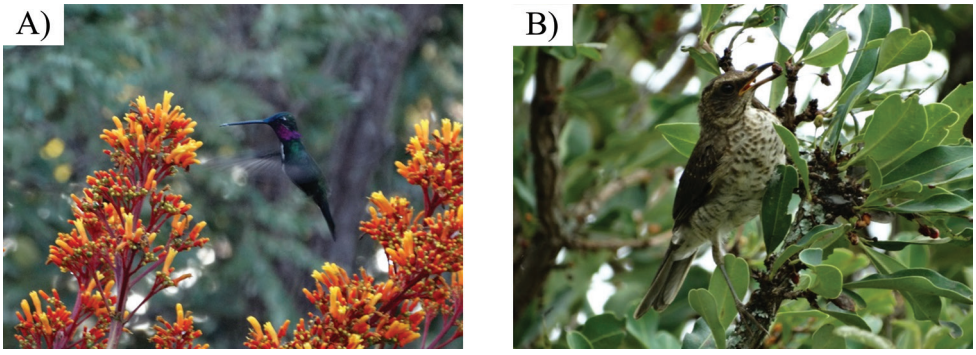

Figure 3. Ornithophily (Bird pollination) and zoochory (animal dispersal) records in the Rupestre Cerrado of Rio Paranaíba, Minas Gerais, Brazil. (**A**) *Heliomaster squamosus* (Apodiformes, Trochilidae) hummingbird with a beak full of nectar, pollinating a *Palicourea rigida* (Gentianales, Rubiaceae) individual. (**B**) *Turdus amaurochalinus* (Passeriformes, Turdidae) individual consuming *Erythroxylum suberosum* (Malpighiales, Erythroxylaceae) fruit. Photo credit: Cássio Cardoso Pereira.

cording to the specialization of the interaction (Zamora-Gutierrez et al. 2021). The elimination of disperser animals, on the other hand, can have negative effects on seedling recruitment, and understanding the plant/animal relationship is crucial in conservation programs and reforestation plans (Pérez-Méndez et al. 2016; Török et al. 2020). Therefore, the conservation of fragments of different sizes, as well as the establishment of corridors to connect landscapes, are very important measures to re-establish the animal populations and ensure the continuous regeneration of these communities (Tabarelli and Gascon 2005; Fontúrbel et al. 2017).

Conclusion

Anthropogenic pressure on this vegetation is the main threat to pollination and dispersal interactions. Despite the risk, the conservation and management of these fragments can contribute to the maintenance of pollination and dispersal services in the cerrados immersed in agricultural landscapes. Thus, this study provides important data on pollination and dispersal services associated with the Cerrado Rupestre and contributes to a better understanding of the functionality and availability of resources in the community, providing indispensable information for the conservation, management, and restoration of natural environments.

Acknowledgements

The authors would like to thank UFV, UFMG and CAPES for their continuous support. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

References

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift (Berlin) 22(6): 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Amico GC, Aizen MA (2005) Seed dispersal by birds in a temperate forest of southern South America: Who disperses to whom? Ecología Austral 15: 89–100.

Barbosa AAA, Sazima M (2008) Biologia reprodutiva de plantas herbáceo-arbustivas de uma área de campo sujo de cerrado. In: Sano SM, de Almeida SP, Ribeiro JF (Eds) Cerrado: ecologia e flora. Embrapa, Brasília, 291–307.

Barroso GM, Morim MP, Peixoto AL, Ichaso CLF (1999) Frutos e sementes – morfologia aplicada à sistemática de dicotiledôneas. Editora UFV, Viçosa, 444 pp.

Bauer DM, Wing IS (2010) Economic consequences of pollinator declines: A synthesis. Agricultural and Resource Economics Review 39(3): 368–383. https://doi.org/10.1017/S1068280500007371

Borchardt KE, Morales CL, Aizen MA, Toth AL (2021) Plant-pollinator conservation from the perspective of systems-ecology. Current Opinion in Insect Science 47(5): 154–161. https://doi.org/10.1016/j.cois.2021.07.003

Carvalho FA (2010) Síndromes de dispersão de espécies arbóreas de florestas ombrófilas submontanas do estado do Rio de Janeiro. Revista Árvore 34(6): 1017–1023. https://doi.org/10.1590/S0100-67622010000600007

Cordero-Schmidt E, Maruyama PK, Vargas-Mena JC, Pereira Oliveira P, de Assis R, Santos F, Medellín RA, Rodriguez-Herrera B, Venticinque EM (2021) Bat–flower interaction networks in Caatinga reveal generalized associations and temporal stability. Biotropica 53(6): 1546–1557. https://doi.org/10.1111/btp.13007

Danieli-Silva A, de Souza JMT, Donatti AJ, Campos RP, Vicente-Silva J, Freitas L, Varassin IG (2012) Do pollination syndromes cause modularity and predict interactions in a pollination network in tropical high-altitude grasslands? Oikos 121(1): 35–43. https://doi.org/10.1111/j.1600-0706.2011.19089.x

Dellinger AS (2020) Pollination syndromes in the 21st century: Where do we stand and where may we go? The New Phytologist 228(4): 1193–1213. https://doi.org/10.1111/nph.16793

Diogo IJS, Martins FR, Verola CF, Costa IRD (2016) Variation in plant-animal interactions along an elevational gradient of moist forest in a semiarid area of Brazil. Acta Botanica Brasílica 30(1): 27–34. https://doi.org/10.1590/0102-33062015abb0198

Eisenlohr PV, Felfili JM, Melo MMRF, Andrade LA, Meira-Neto JAA (2015) Fitossociologia no Brasil – Volume 2: Métodos e estudos de casos. Editora UFV, Viçosa, 474 pp.

Faegri K, van der Pijl L (1979) The principles of pollination ecology. Pergamon Press, Oxford, 244 pp. https://doi.org/10.1016/B978-0-08-023160-0.50020-7

Flora do Brasil (2020) Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br

Fontúrbel FE, Jordano P, Medel R (2017) Plant-animal mutualism effectiveness in native and transformed habitats: Assessing the coupled outcomes of pollination and seed dispersal. Perspectives in Plant Ecology, Evolution and Systematics 28(1): 87–95. https://doi.org/10.1016/j.ppees.2017.09.003

Françoso R, Guaraldo ADC, Prada M, Paiva AO, Mota EH, Pinto JRR (2014) Phenology and fruit production of *Caryocar brasiliense* Cambess and *Enterolobium gummiferum* (Mart) JF Macbr under different burn regimes. Revista Árvore 38(4): 579–590. https://doi.org/10.1590/S0100-67622014000400001

Fuster F, Traveset A (2020) Importance of intraspecific variation in the pollination and seed dispersal functions of a double mutualist animal species. Oikos 129(1): 106–116. https://doi.org/10.1111/oik.06659

Galetti M, Guevara R, Côrtes MC, Fadini R, Von Matter S, Leite AB, Labecca F, Ribeiro T, Carvalho CS, Collevatti RG, Pires MM, Guimarães Jr PR, Brancalion PH, Ribeiro MC, Jordano P (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340(6136): 1086–1090. https://doi.org/10.1126/science.1233774

Gentry AH (1982) Patterns of Neotropical Plant Species Diversity. In: Hecht MK, Wallace B, Prance GT (Eds) Evolutionary Biology. Springer, Boston, 1–84. https://doi.org/10.1007/978-1-4615-6968-8_1

Google Earth (2021) Google Earth. http://earthgoogle.com/

Gottsberger G, Silberbauer-Gottsberger I (2006) Life in the Cerrado: a South American Tropical Seasonal Vegetation. Vol. II. Pollination and Seed Dispersal. Reta Verlag, Ulm, 383 pp.

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annual Review of Ecology and Systematics 13(1): 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

Hubbell SP (1980) Seed predation and the coexistence of tree species in tropical forests. Oikos 35(2): 214–229. https://doi.org/10.2307/3544429

Ishara KL, Destro GFG, Maimoni-Rodella RCS, Yanagizawa YANP (2008) Composição florística de remanescente de cerrado *sensu stricto* em Botucatu, SP. Brazilian Journal of Botany 31(4): 575–586. https://doi.org/10.1590/S0100-84042008000400004

Jacobi CM, Carmo FF (2008) The Contribution of Ironstone Outcrops to Plant Diversity in the Iron Quadrangle, a Threatened Brazilian Landscape. Ambio 37(4): 324–326. https://doi.org/10.1579/0044-7447(2008)37[324:TCOIOT]2.0.CO;2

Janzen DH (1971) Seed Predation by Animals. Annual Review of Ecology and Systematics 2(1): 465–492. https://doi.org/10.1146/annurev.es.02.110171.002341

Kinoshita LS, Torres RB, Forni-Martins ER, Spinelli T, Ahn YJ, Constâncio SS (2006) Composição florística e síndromes de polinização e de dispersão da mata do Sítio São Francisco, Campinas, SP, Brasil. Acta Botanica Brasílica 20(2): 313–327. https://doi.org/10.1590/S0102-33062006000200007

Kuhlmann M, Fagg CW (2012) Frutos e sementes do Cerrado: atrativos para fauna: guia de campo. Rede de Sementes do Cerrado, Brasília, 360 pp.

Kuhlmann M, Ribeiro JF (2016) Evolution of seed dispersal in the Cerrado biome: Ecological and phylogenetic considerations. Acta Botanica Brasílica 30(2): 271–282. https://doi.org/10.1590/0102-33062015abb0331

Lambers H, de Britto Costa P, Oliveira RS, Silveira FA (2020) Towards more sustainable cropping systems: Lessons from native Cerrado species. Theoretical and Experimental Plant Physiology 32(3): 175–194. https://doi.org/10.1007/s40626-020-00180-z

Martins FQ, Rodrigues GB, Garcia E, Cianciaruso MV (2004) Síndromes de dispersão no componente arbustivo-arbóreo em fragmentos de cerrado, no município de Itirapina, São Paulo. In: Santos FAM, Martins FR, Tamashiro JY (Eds) Relatórios de projetos desenvolvidos na disciplina NE211 Ecologia de campo II do Programa de Pós-graduação em Ecologia, IB, UNICAMP. Editora Unicamp, Campinas, 31–47.

Mendonça RC, Felfili JM, Walter BMT, da Silva Júnior MC, Rezende AV, Filgueiras TS, Nogueira PE, Fagg CW (2008) Flora vascular do bioma Cerrado: checklist com 12.356 espécies. In: Sano SM, Almeida SP, Ribeiro JF (Eds) Cerrado: Ecologia e Flora. Vol. 2. Embrapa Cerrados/Embrapa Informação Tecnológica, Brasília, 421–1279.

Morandi PS, Marimon BS, Marimon-Junior BH, Ratter JA, Feldpausch TR, Colli GR, Munhoz CBR, Silva-Júnior MC, Lima ES, Haidar RF, Arroyo L, Murakami AA, Aquino FG, Walter BMT, Ribeiro JF, Françoso R, Elias F, Oliveira EA, Reis SM, Oliveira B, Neves EC, Nogueira DS, Lima HS, Carvalho TP, Rodrigues SA, Villarroel D, Felfili JM, Phillips OL (2020) Tree diversity and above-ground biomass in the South America Cerrado biome and their conservation implications. Biodiversity and Conservation 29(1): 1519–1536. https://doi.org/10.1007/s10531-018-1589-8

Munhoz CBR, Felfili JM (2005) Phenology of the herbaceous layer in a campo sujo community in the Fazenda Água Limpa, Federal District, Brazil. Acta Botanica Brasílica 19(4): 979–988. https://doi.org/10.1590/S0102-33062005000400031

Nason JD, Herre EA, Hamrick JL (1998) The breeding structure of a tropical keystone plant resource. Nature 391(6668): 685–687. https://doi.org/10.1038/35607

Ollerton J (2021) Pollinators and Pollination: Nature and Society. Pelagic Publishing Ltd, Oxford, 289 pp. https://doi.org/10.53061/JAOK9895

Ollerton J, Alarcón R, Waser NM, Price MV, Watts S, Cranmer L, Hingston A, Peter C, Rotenberry J (2009) A global test of the pollination syndrome hypothesis. Annals of Botany 103(9): 1471–1480. https://doi.org/10.1093/aob/mcp031

Patel V, Pauli N, Biggs E, Barbour L, Boruff B (2021) Why bees are critical for achieving sustainable development. Ambio 50(1): 49–59. https://doi.org/10.1007/s13280-020-01333-9

Pereira CC, Santos Soares FF, Fonseca RS, Henriques NR, Arruda DM (2019) Ferruginous Rupestrian Savannah: A floristic and structural analysis of these rare environments. Neotropical Biology and Conservation 14(4): 381–397. https://doi.org/10.3897/neotropical.14.e47228

Pérez-Méndez N, Jordano P, García C, Valido A (2016) The signatures of Anthropocene defaunation: Cascading effects of the seed dispersal collapse. Scientific Reports 6(1): 1–9. https://doi.org/10.1038/srep24820

Pijl L (1982) Principles of dispersal in higer plants. Springer-Verlag, Berlin, 218 pp.

Pinheiro F, Ribeiro JF (2001) Síndromes de dispersão de sementes em Matas de Galeria do Distrito Federal. In: Ribeiro JF, Fonseca CEL, Sousa-Silva JC (Eds) Cerrado: caracterização e recuperação de Matas de Galeria. Embrapa Cerrados, Planaltina, 335–361.

Quirino ZGM, Machado IC (2014) Pollination syndromes in a Caatinga plant community in northeastern Brazil: Seasonal availability of floral resources in different plant growth habits. Brazilian Journal of Biology 74(1): 62–71. https://doi.org/10.1590/1519-6984.17212

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Rabeling SC, Lim JL, Tidon R, Neff JL, Simpson BB, Pawar S (2019) Seasonal variation of a plant-pollinator network in the Brazilian Cerrado: Implications for community structure and robustness. PLoS ONE 14(12): e0224997. https://doi.org/10.1371/journal.pone.0224997

Resende FM, Cimon-Morin J, Poulin M, Meyer L, Loyola R (2019) Consequences of delaying actions for safeguarding ecosystem services in the Brazilian Cerrado. Biological Conservation 234(1): 90–99. https://doi.org/10.1016/j.biocon.2019.03.009

Rocca MA, Sazima M (2010) Beyond hummingbird-flowers: The other side of ornithophily in the neotropics. Oecologia Australis 14(1): 67–99. https://doi.org/10.4257/oeco.2010.1401.03

Rosas-Guerrero V, Aguilar R, Martén-Rodríguez S, Ashworth L, Lopezaraiza-Mikel M, Bastida JM, Quesada M (2014) A quantitative review of pollination syndromes: Do floral traits predict effective pollinators? Ecology Letters 17(3): 388–400. https://doi.org/10.1111/ele.12224

Schupp E, Fuentes M (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. Ecoscience 2(3): 267–275. https://doi.org/10.1080/11956860.1995.11682293

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: A conceptual review. The New Phytologist 188(2): 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x

Silva CID, Araújo G, Oliveira PEAMD (2012) Distribuição vertical dos sistemas de polinização bióticos em áreas de cerrado sentido restrito no Triângulo Mineiro, MG, Brasil. Acta Botanica Brasílica 26(4): 748–760. https://doi.org/10.1590/S0102-33062012000400004

Silveira FA, Negreiros D, Barbosa NP, Buisson E, Carmo FF, Carstensen DW, Conceição AA, Cornelissen TG, Echternacht L, Fernandes GW, Garcia QS, Guerra TJ, Jacobi CM, Lemos-Filho JP, Stradic SL, Morellato LPC, Neves FS, Oliveira RS, Schaefer CE, Viana PL, Lambers H (2016) Ecology and evolution of plant diversity in the endangered campo rupestre: A neglected conservation priority. Plant and Soil 403(1): 129–152. https://doi.org/10.1007/s11104-015-2637-8

Tabarelli M, Gascon C (2005) Lessons from fragmentation research: Improving management and policy guidelines for biodiversity conservation. Conservation Biology 19(3): 734–739. https://doi.org/10.1111/j.1523-1739.2005.00698.x

Toppa RH, Pires JSR, Durigan G (2004) Flora lenhosa e síndromes de dispersão nas diferentes fisionomias da vegetação da Estação Ecológica de Jataí, Luiz Antônio, São Paulo. Hoehnea 32(1): 67–76.

Török P, Bullock James MJM, Jiménez-Alfaro B, Sonkoly J (2020) The importance of dispersal and species establishment in vegetation dynamics and resilience. Journal of Vegetation Science 31(6): 935–942. https://doi.org/10.1111/jvs.12958

Valenta K, Nevo O (2020) The dispersal syndrome hypothesis: How animals shaped fruit traits, and how they did not. Functional Ecology 34(6): 1158–1169. https://doi.org/10.1111/1365-2435.13564

Vander Wall SB, Longland WS (2004) Diplochory: Are two seed dispersers better than one? Trends in Ecology & Evolution 19(3): 155–161. https://doi.org/10.1016/j.tree.2003.12.004

Vieira DL, Aquino FG, Brito MA, Fernandes-Bulhão C, Henriques RP (2002) Síndromes de dispersão de espécies arbustivo-arbóreas em cerrado *sensu stricto* do Brasil Central e savanas amazônicas. Brazilian Journal of Botany 25(2): 215–220. https://doi.org/10.1590/S0100-84042002000200009

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77(4): 1043–1060. https://doi.org/10.2307/2265575

Wunderlee JM (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99(1): 223–235. https://doi.org/10.1016/S0378-1127(97)00208-9

Yamamoto LF, Kinoshita LS, Martins FR (2007) Síndromes de polinização e de dispersão em fragmentos da Floresta Estacional Semidecídua Montana, SP, Brasil. Acta Botanica Brasílica 21(3): 553–573. https://doi.org/10.1590/S0102-33062007000300005

Yamamoto M, Barbosa AAA, Oliveira PEAM (2010) A polinização em cultivos agrícolas e a conservação das áreas naturais: O caso do maracujá-amarelo (*Passiflora edulis* F. *flavicarpa* Deneger). Oecologia Australis 14(01): 174–192. https://doi.org/10.4257/oeco.2010.1401.10

Zamora-Gutierrez V, Rivera-Villanueva AN, Martinez Balvanera S, Castro-Castro A, Aguirre-Gutiérrez J (2021) Vulnerability of bat–plant pollination interactions due to environmental change. Global Change Biology 27(14): 3367–3382. https://doi.org/10.1111/gcb.15611